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# Wild geese do not increase flight behaviour prior to migration

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**Hypertrophy of the flight muscles is regularly observed in birds prior to long-distance migrations. We tested the hypothesis that a large migratory bird would increase flight behaviour prior to migration, in order to cause hypertrophy of the flight muscles, and upregulate key components of the aerobic metabolic pathways. Implantable data loggers were used to record year-round heart rate in six wild barnacle geese (*Branta leucopsis*), and the amount of time spent in flight each day was identified. Time in flight per day did not significantly increase prior to either the spring or the autumn migration, both between time periods prior to migration (5, 10 and 15 days), or when compared with a control period of low activity during winter. The lack of significant increase in flight prior to migration suggests that approximately 22 min per day is sufficient to maintain the flight muscles in condition for prolonged long-distance flight. This apparent lack of a requirement for increased flight activity prior to migration may be attributable to pre-migratory mass gains in the geese increasing workload during short flights, potentially prompting hypertrophy of the flight muscles.**

**Keywords:** barnacle geese; body mass increase; endogenous control; migration; muscle hypertrophy

## 1. INTRODUCTION

Migratory birds have been shown to exhibit extreme phenotypic plasticity [1]. Prior to migration, organs such as the digestive system and liver may atrophy significantly, whereas the heart and pectoralis flight muscle hypertrophy [2]. These changes optimize flight capability during migration, while avoiding transport of unnecessary mass [3]. Based on human muscle responses to hyper- and hypodynamy, it has been assumed that hypertrophy of avian muscle must be preceded by exercise and increased use [4]. However, evidence now exists to the contrary and suggests that in captive birds at least, their muscles have the capacity to hypertrophy and atrophy without any change in muscle use or exercise levels. These changes are largely independent of the external

environment or behaviour [5,6]. This suggests that changes in muscle architecture can not only be a result of increased exercise [7], but some birds may also have an endogenous capacity for muscle hypertrophy [5,6]. However, this theory has yet to be tested in birds free to behave normally.

An example of a long-distance migrant is the Svalbard population of barnacle geese (*Branta leucopsis*), which migrate 2500 km each autumn from their breeding grounds in Spitsbergen to the Solway Firth, southwest Scotland [8]. Previously, it has been demonstrated in barnacle geese that wild flighted birds have significantly higher levels of key components of the aerobic metabolic pathway, such as citrate synthase (CS), 3 $\beta$ -hydroxacyl-CoA dehydrogenase (HAD) and fatty-acid binding proteins (FABP) in comparison with both captive and juvenile birds that had never flown [9,10]. Moreover, these components are upregulated shortly before migration [9,10]. Similar observations have been noted in migratory passerines and shorebirds, where CS, HAD and FABP are upregulated by up to 110 per cent prior to migration [11,12]. The difference in levels of observed CS, HAD and FABP between flightless and volant geese does suggest that a certain amount of flight activity is vital for the maintenance of flight muscles, and that for optimal flight performance such as that required during migration, the composition of the muscle can be as important as the muscle mass [9,10]. As such, it has been predicted that long-distance migrants should increase both flight muscle mass and upregulate enzymes such as CS and HAD [12] prior to migration, possibly through engaging in anticipatory flight behaviour. To investigate this further, we used a biologging approach to identify periods of flight in wild unmanipulated barnacle geese by recording heart rate ( $f_H$ ) continuously throughout the annual cycle [8,13]. Heart rate increases dramatically during flight, making periods of flight easily identifiable from  $f_H$  traces [8,13]. We predicted that free-ranging geese increase their flight activity prior to migration. This flight increase would cause hypertrophy of the flight muscles and upregulate essential enzymes for aerobic metabolism.

## 2. MATERIAL AND METHODS

### (a) *Birds and heart rate measurements*

Eight wild barnacle geese were caught at Ny-Ålesund research station 'Spitsbergen' (78°55' N, 11°56' E, 78.917° N, 11.933° E) during the flightless period (July 1999) of wing moult. Heart rate was measured continuously throughout the annual cycle by custom-made implantable heart rate data loggers [8,13,14]. The loggers were programmed to record  $f_H$  every 5 s. Methods for logger implantation and removal are described in detail elsewhere [8,13,14]. All implanted geese were colour-ringed to aid recapture the following year. Recordings of  $f_H$  for a minimum of 10 months that covered both the spring and autumn migration periods were obtained from all six birds that were recaptured in the summer of 2000.

### (b) *Flight activity*

The frequency distribution of  $f_H$  for each goose was examined to determine a threshold which would identify periods of flight (see also [8,13]). The result was a bimodal distribution with  $f_H$  values ranging from 40 to 180 b.p.m. assumed to be ground non-flight activities, and values of approximately 285–400 b.p.m. that were associated with flight (see also [8]). A custom-written program then processed the data to calculate time in flight for each day for each goose.

Using the full record of time in flight per day for each goose, the annual cycle was divided into seven distinct phases (figure 1) based on the  $f_H$  values: (i) winter, (ii) pre-spring migration, (iii) spring migration, (iv) breeding, (v) wing moult, (vi) pre-autumn migration

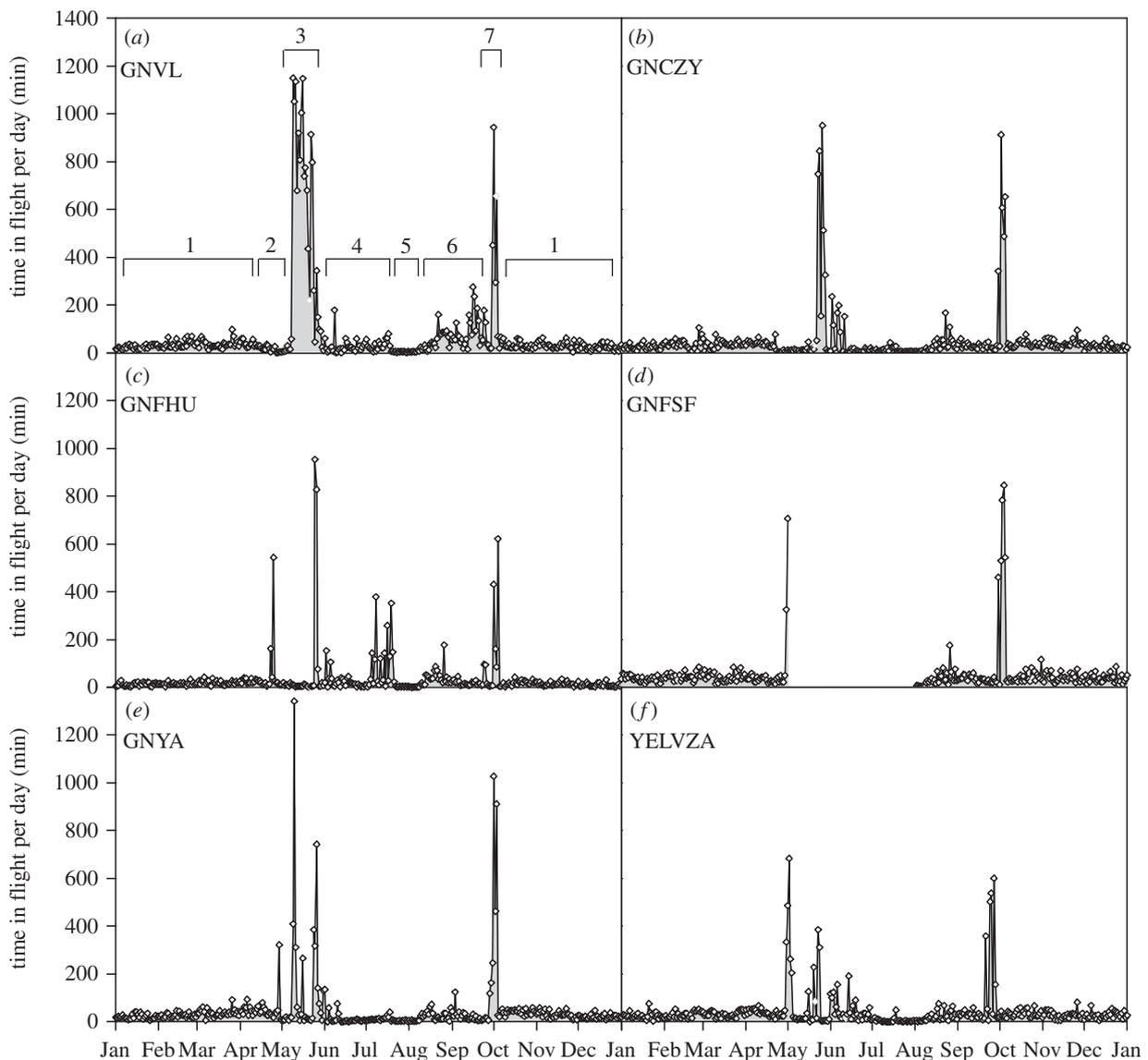


Figure 1. (a–f) Time in flight per day throughout the annual cycle of six barnacle geese. The year is split into seven distinct cycles: (1) winter, (2) pre-spring migration, (3) spring migration, (4) breeding, (5) wing moult, (6) pre-autumn migration and (7) autumn migration. The seven phases are highlighted in (a). The difference in duration of the spring and autumn migration is well documented in barnacle geese [15].

and (vii) autumn migration. Each migration departure was identified as the first flight with duration of over 30 min. The pre-migratory period was identified as the period 15 days prior to the first migratory flight. The flightless period of wing moult was also clear from the absence of any flight. The end of migration was identified from the absence of flight behaviour over 30 min per day. Mean time in flight per day was calculated for each bird for three periods prior to the migrations: 0–5, 6–10 and 11–15 days (i.e. within phases 2 and 6). These were compared with each other and a control period (winter, phase 1), a time of known low-flight activity. A subsequent analysis compared these pre-migratory periods between the spring and autumn pre-migration. For both analyses, a general linear model was used with goose identification as a random factor, and  $\alpha < 0.05$ .

### 3. RESULTS

Periods of flight were easily identified from the  $f_H$  data taken from the data loggers (figure 1). Prior to spring migration, there was no difference in time in flight (per day) between the periods identified prior to migration, or when compared with the control period ( $F_{3,15} = 1.08$ ,  $p = 0.39$ ; figure 2a). There was, however, a difference in time in flight per day between the individual geese ( $F_{5,15} = 3.5$ ,  $p = 0.027$ ). Similarly, in autumn

there was no difference in time in flight per day between the time periods identified prior to migration ( $F_{3,15} = 0.95$ ,  $p = 0.44$ ; figure 2b), although again there was a difference between individuals ( $F_{5,15} = 6.06$ ,  $p = 0.0003$ ). When the two pre-migratory periods were combined in a single analysis, there was no significant interaction between migratory period and flight duration ( $F_{2,25} = 0.84$ ,  $p = 0.44$ ). When this interaction was eliminated, there was no difference in time in flight per day between the two pre-migratory periods ( $F_{1,27} = 2.14$ ,  $p = 0.15$ ).

### 4. DISCUSSION

The wild geese did not significantly increase flight behaviour prior to the spring or autumn migrations. Although the muscle masses of the birds in the present study were not measured, it is likely the geese experienced flight muscle hypertrophy prior to the migratory period, as flight muscle hypertrophy has been documented in both wild and captive barnacle geese [6,9,10,16] and

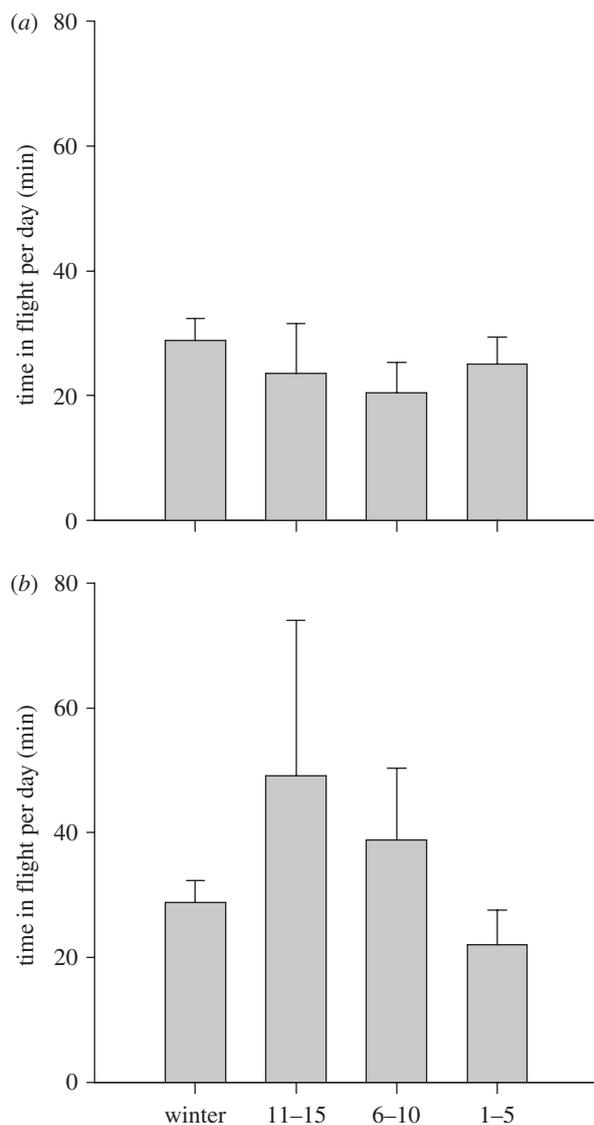


Figure 2. Mean ( $\pm$  s.e.m.) time in flight per day by six barnacle geese during winter, compared with flight time (days) between periods prior to the (a) spring and (b) autumn migration.

many other species of birds [12,17–19]. Marsh [17] documented pre-migratory flight muscle hypertrophy in grey catbirds (*Dumetella carolinensis*) and demonstrated that the increase in flight muscle mass was highly correlated with the pre-migratory increase in body mass that was recorded. Similarly, Cooper's hawks (*Accipiter cooperii*) and red knots (*Calidris canutus*) show the same pattern of associated body mass gain and flight muscle hypertrophy [18,19]. It is possible, therefore, that pre-migratory mass gains cause hypertrophy of the flight muscles by increasing wing loading [18]. Consequently, the pre-migratory increase in body mass in wild barnacle geese [8] would act to cause hypertrophy of the flight muscles during the 22 min per day spent in flight, and no increase in flight time would be required. Therefore, rather than spending more time in flight per day, the rise in body mass increases workload on the flight muscles through increased wing loading, causing muscle hypertrophy and potentially upregulating CS, HAD and FABP.

There is evidence to suggest that flight muscles have the capacity to hypertrophy without an increase

in use or a simultaneous increase in body mass [6]. It is possible that this endogenous capacity for muscle hypertrophy observed in waterfowl previously ([6], see also [20]) may have contributed to the apparent lack of requirement for increased flight and muscle training prior to migration. Moulting captive barnacle geese, for example, experience a significant atrophy of their flight muscles at the onset of wing moult, which occurs simultaneously with a dramatic decrease in body mass [6]. Mid moult, however, flight muscles begin to hypertrophy while body mass continues to decrease, and this hypertrophy is not accompanied by an increase in wing-flapping behaviour ([6], see also [21]). In the present study, we could not use  $f_H$  to reliably detect ground-based wing-flapping behaviour in the wild geese, only instances of flight. However, as wing flapping is a ground-based activity and does not involve additional load bearing, it would not be expected to cause hypertrophy of the muscles to such an extent as powered flight, and particularly not in response to gains in body mass. Hypertrophy of the flight muscles of goslings has been proposed to be a direct consequence of ground-based wing-flapping behaviour [9,10,16]. However, despite experiencing muscle hypertrophy, levels of CS, HAD and FABP in goslings were significantly lower than in adult geese, suggesting some degree of flight is important for the maintenance of the metabolic pathways in the flight muscle (but see also [21]). This suggests that different mechanisms may be at work within the same species at different times throughout the annual cycle, depending on the requirements and available resources. In the present study, it appears that mechanisms such as body mass gain may potentially ensure there is no requirement for an increase in time spent flying prior to migration in this species, and it is apparent that energetically costly flight behaviour is avoided in order to preserve fat stores that have been built up for the longer, more arduous, migratory journeys.

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